

Research

Habitat characteristics and species interference influence space use and nest-site occupancy: implications for social variation in two sister species

Claire M. S. Dufour, Neville Pillay, Nico Avenant, Johan Watson, Etienne Loire and Guila Ganem

C. M. S. Dufour (<http://orcid.org/0000-0003-2270-938X>) (clairems.dufour@gmail.com) and G. Ganem (<http://orcid.org/0000-0002-5244-4979>), ISEM, CNRS, Univ. of Montpellier, IRD, EPHE, Montpellier, France. – CMSD, GG and N. Pillay, School of Animal, Plant and Environmental Science, Univ. of the Witwatersrand, Wits, South Africa. Present address for CMSD: Museum of Comparative Zoology, Dept of Organismic and Evolutionary Biology, Harvard Univ., Cambridge, MA, USA. – N. Avenant, Dept of Mammalogy, National Museum, and Centre for Environmental Management, Univ. of the Free State, Bloemfontein, South Africa. – J. Watson, Dept of Economic Development, Tourism and Environmental Affairs, Biodiversity Research, Bloemfontein, South Africa. – E. Loire, Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD), UMR, CMAEE, C2B, Montpellier, France.

Oikos

128: 503–516, 2019

doi: 10.1111/oik.05357

Subject Editor: Ben Chapman

Editor-in-Chief: Dries Bonte

Accepted 23 October 2018

Nest-site selection is an important component of species socio-ecology, being a crucial factor in establishment of group living. Consequently, nest-site characteristics together with space-use proxies may reveal the social organization of species, which is critical when direct observation of social interactions is hindered in nature. Importantly, nest-site choice is expected to be under strong selective pressures and the object of intra- and interspecific competition. Although the bulk of research on sociality focuses on its ecological drivers, our study introduces interspecific competition as a potential factor that could influence social evolution. We investigated the influence of habitat and interspecific competition on the social organization of two sister species of the African four striped mouse, *Rhabdomys dilectus dilectus* and *Rhabdomys bechuanae*, in a similar macroenvironment. These species diverged in allopatry and occupy distinct environmental niches. We radiotracked 140 adults to identify their nest-sites, determine nest characteristics and record groups that shared nest-sites. Group cohesion was estimated from nest-site fidelity, group association strength, and home range overlap within versus between group members. We compared the two species in sympatry versus parapatry to determine the impact of species interference on sociality. In parapatry, the two species selected distinct nest-site types, interpreted as different anti-predator strategies: *R. bechuanae* selected fewer, spaced, less concealed nest-sites whereas *R. d. dilectus* selected clumped and less visible nest-sites. *Rhabdomys bechuanae* also showed more cohesive and stable social groups than *R. d. dilectus*. In sympatry, compared to *R. bechuanae*, *R. d. dilectus* occupied similar nest-sites, however slightly more exposed and clumped, and displayed similar nest-site fidelity and group association strength. We conclude that although habitat selection may be an important driver of social divergence in *Rhabdomys*, species interference, by limiting *R. d. dilectus* movements and forcing nest-site sharing may induce new ecological pressures that could influence its social evolution.

Keywords: habitat selection, home range overlap, interspecific competition, nest-site sharing, radiotracking, *Rhabdomys*, secondary contact, social groups

Introduction

Nest-sites are important components of the habitat requirements of species, and generally of their socio-ecology (Santos and Lacey 2011, Webber and Vander Wal 2018). Being critical environmental features for survival and reproduction (Edelman et al. 2009, Auclair et al. 2014), nest-site choice is expected to be under strong selection pressure (Forstmeier and Weiss 2004, Mainwaring et al. 2017), and the object of both intra- and interspecific competition (Schradin 2005, Duckworth et al. 2015).

Nest-sites are crucial resources for the establishment and maintenance of group-living in many species (e.g. rodents, Lacey and Sherman 2007, Ebensperger et al. 2008, Santos and Lacey 2011; birds, Banda and Blanco 2009, Duckworth et al. 2015; and, insects, Rangel et al. 2010). Moreover, group members establish bonds and sometimes breed communally (Hayes 2000, Schradin 2013, Auclair et al. 2014) in nest-sites that they defend and compete for against other groups (e.g. *Peromyscus* sp., Dooley and Dueser 1996; *Pseudophryne bibronii*, Heap and Byrne 2013; *Rhabdomys pumilio*, Schradin et al. 2006). When social interactions are difficult to observe directly in nature, proxies such as nest-site occupancy could be particularly helpful in revealing the social organization (i.e. the size, sexual composition and spatiotemporal cohesion of a group; Kappeler and Schaik van 2002) of cryptic species (Radespiel et al. 2003, Schradin 2013). For example, multiple occupancy of a nest-site could indicate group living. Further, nest-site switching is expected to be less costly for solitary species, because it involves a single individual's decision, compared to social groups where individuals are expected to show higher nest-site fidelity and group association strength (Hayes 2000). Finally, combining space use and nest-site occupancy studies could help to further elucidate group membership in cryptic species: e.g. home range overlaps are expected to be greater for members within than between groups (Mappes et al. 1995, Atwood and Weeks 2003, Stow and Sunnucks 2004, Schradin and Pillay 2005).

By coupling space use proxies with nest-site characteristics and occupancy, our study aims to elucidate how local habitat characteristics and species interference influence spatial group establishment and therefore its social organization. Competition between sister species is known to impact resource use (Dufour et al. 2017), reproduction (Pfennig and Pfennig 2009) and agonistic interactions (Latour and Ganem 2017), enhancing species divergence or convergence in sympatry (Grant 1972, Grether et al. 2009) or resulting in the exclusion of one of the species (Violle et al. 2011). Species interference has been largely neglected in the study of sociality. It is crucial to recognize however, that interspecific competition may directly alter social behavior, because it may drive shifts in resource use (such as nest-site selection), as shown in colonies of native and invasive fire ants (*Solenopsis* sp.) in the USA (Holway and Suarez 1999). This competitive pressure may be particularly important when the two competing species are closely related since they are expected to

exploit similar resources (Violle et al. 2011) and display similar behaviors (Lichtenstein et al. 2017). Moreover, although environmental impact on social variation within and between species has been the focus of much research (reviewed by Lacey and Sherman 2007, Silk 2007, Gardner et al. 2015), few have addressed the impact of microhabitat variations on sociality, particularly in cryptic species.

Here, we studied two species of the African four striped mouse, *Rhabdomys dilectus dilectus* and *Rhabdomys bechuanae*, which have distinct environmental niches in southern Africa, where they diverged in allopatry (du Toit et al. 2012, Meynard et al. 2012, Dufour et al. 2015a). The distributions of the two species overlap partially in the central part of South Africa (Fig. 1 here; Dufour et al. 2015a), forming patches of parapatric (i.e. biogeographically abutting monospecific populations) and sympatric (i.e. mixed-species) populations within the same macroenvironment (Ganem et al. 2012, Dufour et al. 2015a). In allopatry (i.e. monospecific populations distant from contact areas), *R. d. dilectus* occurs predominantly in mesic areas and occupies habitats of continuous vegetative cover, while *R. bechuanae* occurs in arid to semi-arid areas with more patchily distributed cover. In parapatry, *R. d. dilectus* is mostly found in riverine vegetation with dense cover, whereas *R. bechuanae* uses patchy open shrubland vegetation (Dufour et al. 2015a). In sympatry, *R. d. dilectus* still appears to select microhabitats with more cover than *R. bechuanae* (Dufour et al. 2015a). Importantly, in sympatry, home range overlaps between the two species are more restricted than expected, suggesting avoidance due to interspecific competition (Dufour et al. 2015a). Having been recognized only recently (du Toit et al. 2012), our knowledge of the specific biology of these two species is largely unknown (Dufour et al. 2015a, Supplementary material Appendix 1 Table A1). Nonetheless, all *Rhabdomys* species are diurnal and previous studies also suggested that *R. bechuanae* (sleeping and breeding in shrub nests) would be more social than *R. d. dilectus* (sleeping and breeding in covered grass nests) in allopatry (Supplementary material Appendix 1 Table A1). Moreover, *R. bechuanae* has larger home ranges (Dufour et al. 2015a) and is considered to be bolder (because it exploits open habitats more exposed to predation) than *R. d. dilectus* which avoids open habitats even when supplemented with food (Abu Baker and Brown 2010).

The conditions in the areas where the two species distributions abut allow for comparisons of their social organization in similar climatic, latitudinal and altitudinal conditions, as well as in the presence or absence of interspecific competition. Few systems offer such natural experimental settings, as in our study system, to test the role of local habitat characteristics and species interference on species social divergence.

We used a population-level approach, testing 11 parapatric and three sympatric populations of the two species, and adopted an indirect method to assess sociality using spatial and nest-site occupancy proxies. Nest-sites were considered as a critical resource, particularly in the context of

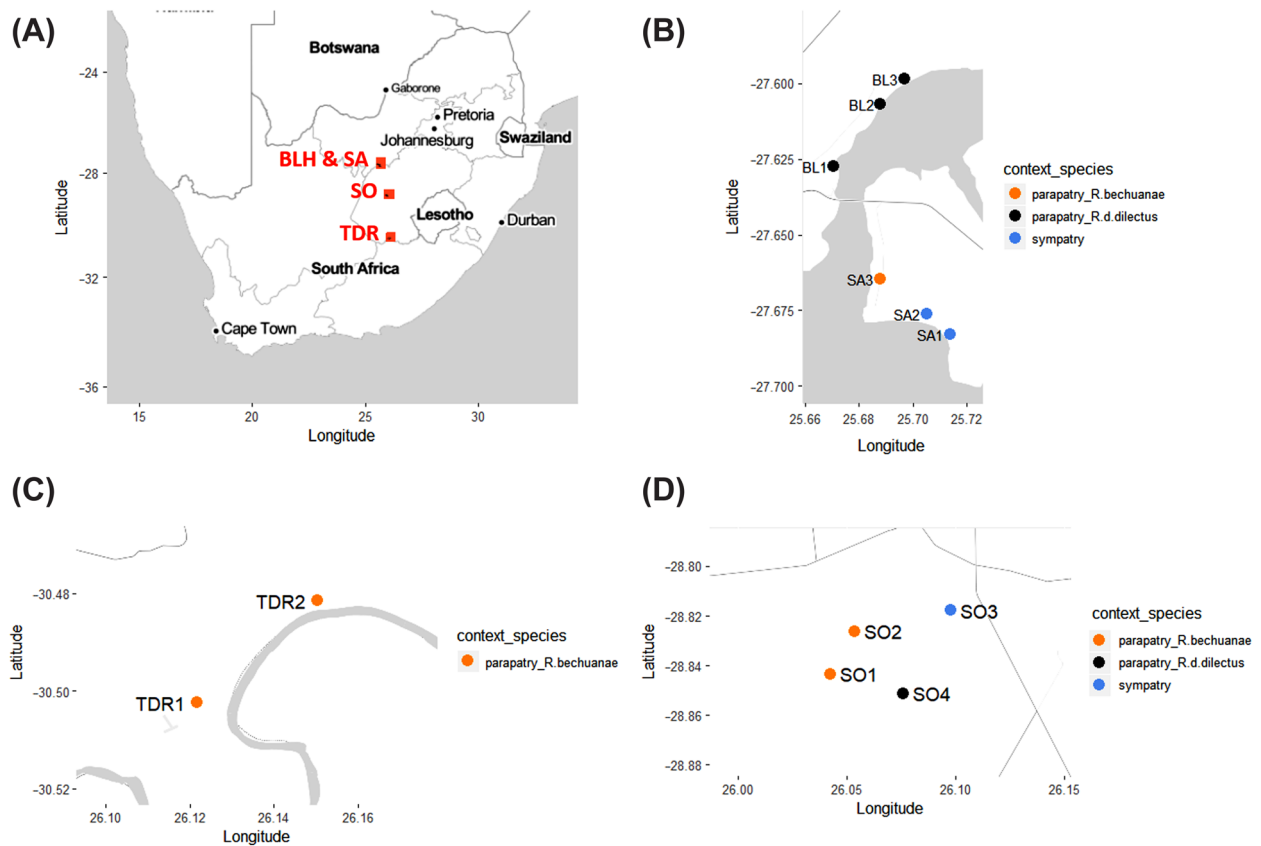


Figure 1. Study area in South Africa (A) – Bloemhof (BLH), Sandveld (SA), Soetdoring (SO) and Tussen die Riviere (TDR) Nature reserves – and details of the distribution of the sites sampled in BLH and SA (B), TDR (C) and SO reserves (D) according to species occurrence (parapatry and sympatry of *R. bechuanae* and *R. d. dilectus*). The TDR1 and SA2 sites were resampled (TDR1 in 2012 and 2013 where parapatric *R. bechuanae* occurred; SA2 in 2011 was sympatric and became parapatric for *R. bechuanae* in 2012).

intra- and interspecific competition. We radiotracked adult striped mice during the breeding season (when intraspecific reproductive competition is expected to peak; Schoepf and Schradin 2012) to locate their nest-sites. Since the characteristics of nest-sites and their accessibility to predators (e.g. safe cover versus risky open sites) can influence survival (Kotler et al. 1991, Schooley et al. 1996, Ebensperger et al. 2008), we assessed the distribution and external features of occupied nest-sites and also determined nest-site fidelity and group association strength. Moreover, we ascertained group membership and cohesion by assessing home range overlaps, which were expected to be the highest between group members (Mappes et al. 1995, Atwood and Weeks 2003, Schradin and Pillay 2004).

We tested two hypotheses: 1) patchily distributed nest-sites are expected to induce spatial grouping of individuals with high group association strength and nest-site fidelity (Atwood and Weeks 2003, Schradin and Pillay 2004). Since *R. bechuanae* occurs in open-shrubland type habitats and *R. d. dilectus* occurs in habitats with more continuous cover in allopatry and parapatry (Supplementary material Appendix 1 Table A1; Dufour et al. 2015a), different constraints on their nest-site characteristics and distribution could influence

their social organization: *R. bechuanae* is expected to show more cohesive groups than *R. d. dilectus* in parapatry. In addition, we also expect the two species to have similar social organization in sympatry, where they both occupy open-shrubland habitats (Dufour et al. 2015a). 2) Species interference could induce further pressure on space use, microhabitat selection (Dufour et al. 2015a, 2017) and nest-site occupancy (Dooley and Dueser 1996, Duckworth et al. 2015). In our study system, interspecific interference was suggested by the low home range overlaps between the species in sympatry (Dufour et al. 2015a). *Rhabdomys bechuanae* occupies similar microhabitats in the two biogeographical contexts, and hence any shift in its social organization in sympatry, as compared to parapatry, might be ascribed to interference with *R. d. dilectus*. Since *R. d. dilectus* occupies different microhabitats in parapatry and sympatry, both microhabitats and species interference could interact to shape its social organization. Yet, if species interference influenced *R. d. dilectus* social organization we would expect changes in space use (e.g. more clumped or less clumped nest-sites compared to *R. bechuanae*) or the quality of selected nest-sites (e.g. worse or better than *R. bechuanae*). In Table 1, we summarized the hypotheses, predictions and results.

Table 1. A synthesis of the two hypotheses tested in the study, the traits used to test them, the predicted outcomes in parapatry and sympatry in *R. d. dilectus* and *R. bechuanae*, and a brief summary of the results.

Hypotheses	Measured traits	Predictions				Results
		<i>R. d. dilectus</i>		<i>R. bechuanae</i>		
1. Microhabitat and nest-site selection drive social organization in <i>Rhabdomys</i>	nest-site characteristics	Parapatry	Sympatry	Sympatry	Parapatry	yes
		dense cover in grass with high predation protection clustered	open shrubland with medium to low predation protection patchy	open shrubland with medium to low predation protection patchy	open shrubland with medium to low predation protection patchy	
	nest-site distribution					yes (in parapatry for both species) no (in sympatry for <i>R. d. dilectus</i>)
	nest-site fidelity group association strength volume of interaction	low low	high high	high high	high high	yes yes
2. Interspecific interference induces new ecological pressures that impact the social organization of <i>Rhabdomys</i> .		intragroup = intergroup	intragroup > intergroup	intragroup > intergroup	intragroup > intergroup	yes (in sympatry for both species) no (in parapatry for <i>R. d. dilectus</i>)
	same traits as above	same predictions as above in parapatry	any deviation from above predictions, leading to species differences in sympatry	same predictions as above in parapatry	same predictions as above in parapatry	yes (in sympatry: <i>R. d. dilectus</i> occupied clustered nest-sites, less protected from predation than <i>R. bechuanae</i>)

Material and methods

Study area

This study took place in four South African nature reserves within the savanna and grassland biomes: Sandveld (SA; S27°43' E25°45'), Soetdoring (SO; S28°50' E26°03') and Tussen die Riviere (TDR; S30°28' E26°09') in the Free State Province, and Bloemhof Dam (BLH; S27°38' E25°40') in the North-West Province (Fig. 1). The study was conducted during the austral spring (October–November 2011, 2012 and 2013), which coincided with the breeding season of *Rhabdomys bechuanae* and *R. d. dilectus* in these areas. In total, 14 populations (several populations per reserve, Table 2, Fig. 1) were sampled in 14 sites (hereafter study sites), separated by a minimum of 1 km from each other (details provided in Dufour et al. 2015a).

Trapping procedures

Mice were captured using Sherman and PVC live-traps. Traps were set along lines, with a distance of approximately 10 m between traps (10–30 traps/line). The number of trap lines varied with the study site size (for more details on the procedure and general handling Dufour et al. 2015a). Individuals were marked with ear tags (7 mm, 0.17 g), sexed and measured (body length to the nearest mm). Males were considered as adult when their body length was ≥ 7.8 cm (on the basis of the size of the smallest scrotal male), and females when their body length was ≥ 7.5 cm (i.e. size of the smallest pregnant female). Because the two species could not be distinguished visually, a tail sample (< 1 cm) was collected from each mouse and subsequently used for post hoc species identification, using Cytochrome Oxidase I genotyping (as described in Ganem et al. 2012). The trap lines were maintained for the duration of the radiotracking period. When trapped, a radiotracked mouse was immediately released and no radiotracked mouse spent the night in a trap.

Nest-sites localization and assessment of nest-site sharing

In order to investigate nest-site occupancy, 140 adult striped mice (73 males and 67 females) were radiotracked (an average of 49% of the total adult population trapped was radio-tracked, with about 62% in eight study sites, and 95% in four study sites). They were equipped with VHF collars. Since the striped mouse is diurnal, geo-localization data were collected at sunset (confirmed at sunrise) to locate and confirm nest-sites. A group was identified on the basis of nest-site sharing. In total, 334 nest-sites were identified in 78 sampling nights. Once nest-sites were identified, we placed additional traps (at sunset and checked them at sunrise) at the entrance of a subsample of 36 nest-sites to detect the presence of additional adults, which were not radiotracked during our study, in traps very close to these nest-sites. We found a strong positive correlation (Pearson test: $t = 6.5973$, $df = 34$, $p < 0.001$, $R^2 = 0.75$) between group size obtained by trapping with that obtained by radiotracking, confirming the reliability of our estimation of minimum size of adult groups based on radiotracked individuals. Pairs of two radiotracked adults, sometimes composed of a male and a female, were considered as a group, because we were limited by the number of mice we could radiotrack and hence our index might have under-estimated the actual group size (radiotracked mice that appeared to nest solitarily might have shared their nest with non radiotracked mice). Social groups in the sister species *R. pumilio* were comprised of an adult male and one or more adult females and their progeny of different ages (Schradin and Pillay 2005).

Nest-site characterization

Because nest-sites are important determinants of group living, we assessed the characteristics of nest-sites used by the radiotracked mice from two photographs: one depicting the external features (i.e. entire vegetation

Table 2. Sample size of populations, individuals and nest-sites in this study, as well as radiotracking duration by context (parapatry versus sympatry) and species (*R. bechuanae* and *R. d. dilectus*).

	Parapatry <i>R. d. dilectus</i>	Sympatry	Parapatry <i>R. bechuanae</i>	Total/average
Number of populations (= study sites)	4	3	7	14
Radiotracking duration (mean \pm SD number of days)	11.19 \pm 0.96	14.9 \pm 2.58	12.17 \pm 2.61	12.3 \pm 2.76
Number of nest-sites identified	125	84	125	334
Number of nest-sites characterized	106	58	112	276
Number of radiotracked individuals	45	22 <i>R. bechuanae</i> 14 <i>R. d. dilectus</i>	59	140
Number of mice radiotracked for at least five days	41	18 <i>R. bechuanae</i> 11 <i>R. d. dilectus</i>	47	117
Number of individuals with identified nest-sites	37	14 <i>R. bechuanae</i> 10 <i>R. d. dilectus</i>	44	105
Number of individuals sharing (with another striped mouse) at least one nest-site	41	12 <i>R. bechuanae</i> 5 <i>R. d. dilectus</i>	44	102
Number of adults obtained from traps set within a 4 m zone around each of 36 nest-sites	52	18 <i>R. bechuanae</i> 6 <i>R. d. dilectus</i>	53	129

constituting the nest-site); and the other focusing on the most visible entrance of the nest-site, when visible (Fig. 2). From these photographs, we recorded external features and the state of the vegetation (if any), as well as an index of visibility of the nest-site entrance, assessing whether a snake, mammal carnivore or bird of prey could access the nest entrance (i.e. a measure of protection from predation; Table 3).

Nest-site distribution

The surface area of each of the 14 study sites was small enough (2–19 ha) for an individual striped mouse to traverse entirely during the study period; the longest distance between recaptures of an adult individual was 900 m in our study, and Schradin (2006) showed that both male and female striped mice travel a maximum distance of about 900 m per day. Hence, we hypothesized that all nest-sites identified within a study site could be exploited by any striped mouse, unless constrained by exposure to predators and/or territoriality (intra- and interspecific). To test our hypothesis, we calculated the distance between 1) all nest-sites used by a focal mouse (nest-site network) over a period of at least five days (when the home range size stabilized and reached asymptotic values; Dufour et al. 2015a), and 2) all nest-sites identified within each study site during a radiotracking session. Because of statistical constraints, only study sites in which at least five mice were radiotracked for a period of at least five days were considered here. Hence, a total of 105 radiotracked mice (mean \pm SD distance between nest-sites used by a mouse: 26.1 ± 24.3 m) geo-localized in 312 nest-sites (mean \pm SD distance between nest-sites in a given study site: 124.0 ± 91.5 m) in nine study sites, were considered in this analysis.

Nest-site fidelity

Nest-site fidelity is assumed to characterize group living, and may also be an indication of nest-site attraction. Nest-site fidelity was calculated as the number of different nest-sites occupied by a given individual divided by the number of nights he was radiotracked (at least five nights). This analysis involved 117 mice. In order to validate the appropriateness of this ratio, nest-site fidelity of lactating ($n=14$) and non-lactating ($n=47$) females were compared. Striped mice produce offspring in a nest where pups stay during the lactating period (10–16 days, Pillay 2000). Since pup survival requires suckling, and transport of new-born between relatively distant nest-sites may not occur (Pillay 2000), we expected that lactating females would not risk leaving their progeny alone over-night and hence would show the highest nest-site fidelity. While the distance between utilized nest-sites did not differ between lactating (19.9 ± 12.8 m) and non-lactating females (20.8 ± 16.3 m; Mann–Whitney U test, $W=313$, $p=0.790$), lactating females showed greater nest-site fidelity (0.4 ± 0.1 ; a score of 1 indicating use of a different nest-site each night) than non-lactating females (0.6 ± 0.2 ; $W=557.5$, $p=0.005$), validating the use of our index.

Group association strength based on frequency of nest-site sharing

In order to assess cohesion between adult mice sharing the same nest-site, we calculated an association strength index (AS) derived from VanderWaal et al. (2013). We hypothesized that individuals which shared a nest-site for at least one night during the radiotracking period were part of a group. The association strength index of any group was calculated as

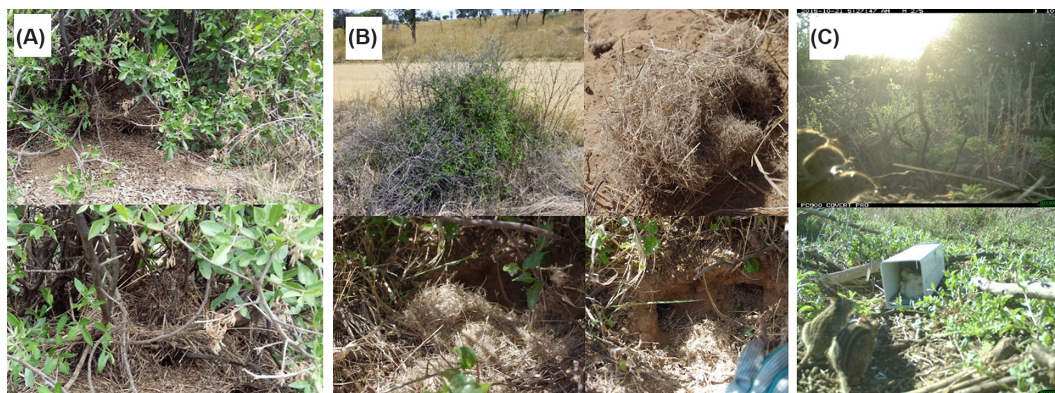


Figure 2. Photographs showing examples of nest-site characteristics and indicating social tolerance in *R. bechuanae*. (A) Nest-site relatively exposed to terrestrial predators, with the bottom image showing details of the nest covered with dead grass beneath a bush. (B) Nest-site that we excavated out at the end of the study. Concealed entrances led to connected burrows and to a large central chamber containing nesting material. This nest-site was occupied by a large group (more than five individuals) of adults as well as juveniles. The central, large chamber contained a large nest made of grass (second from top image in B) within which we found pups and unweaned juveniles. The last image of the panel (bottom right corner; B) shows two independent tunnels with entrances under thick bush that both led to the central chamber. (C) Social behavior captured using a camera trap: the top image taken in a very early morning (5:30 a.m.) shows three mice basking in the early sun (several meters from their nest); the bottom image shows two mice approaching a trap together in the middle of the afternoon.

Table 3. Nest-site characteristics (parameters considered and variables measured) from photographic analysis.

Parameters	Categories	Description
External features	grass	The main vegetation (>50%) around nests was composed of grass, reeds or rushes (e.g. <i>Juncus</i> sp., <i>Digitaria</i> sp., <i>Eragrostis</i> sp.)
	bushy	The main vegetation (>50%) was woody (e.g. <i>Asparagus</i> sp., <i>Acacia</i> sp., <i>Ziziphus</i> sp., <i>Lycium</i> sp.)
	bushy/grass	A mixture of grass (50%) and bush (50%)
	bare soil	No vegetation (a burrow surrounded by bare soil, or a burrow in a termite mound)
Vegetation state	dead	The surrounding vegetation (>50%) was dead, dry and/or uprooted
	alive	The vegetation was alive (>50%)
	mixed	Mixed dead (50%) and alive (50%) vegetation
	none	Only bare soil
Predation protection	low	Birds (e.g. <i>Haliaeetus vocifer</i>), small mammals (e.g. <i>Cynictis penicillata</i>) and snakes (e.g. <i>Bitis arietans</i>) could see the nest entrance and access the nest
	intermediate	Some of the predators might not have access (e.g. entrance visible only from the ground or the entrance was narrow)
	high	The nest-site entrance was completely (100%) hidden and/or presence of obstacles such as dense thorns.

the number of different nest-sites shared by these individuals divided by the number of nest-sites they did not share. For example, if a group was composed of three individuals i , j and k , occupying Y = number of nest-sites, the following formula was applied:

$$AS(i, j, k) = \frac{Y_{\text{shared by } ijk} + Y_{\text{shared by } ij} + Y_{\text{shared by } ik} + Y_{\text{shared by } jk}}{Y_i \text{ without } jk + Y_j \text{ without } ik + Y_k \text{ without } ij}$$

Of the 117 individuals involved in the nest-site fidelity analysis, 102 mice shared at least one nest-site and were included in the group association strength analysis.

Home range overlaps: a validation of group membership

We expected group members to show greater home range overlap than non-group members (Mappes et al. 1995, Atwood and Weeks 2003, Schradin and Pillay 2004). To test this prediction, individual geo-locations (radiotracked points during the day at 7 a.m., 9 a.m., 11 a.m., 2 p.m., 4 p.m. and sunset at 7 p.m.) were used to calculate the individual home range size. Home ranges were defined as the areas encompassed within the 0.95 cumulative isopleth of the utilization distributions (UDs), estimated using the fixed kernel method with the reference smoothing parameter in R software (Worton 1989). Only mice with at least 27 geo-locations over at least five days ($n=111$ mice with stable home ranges) were included in this analysis (Dufour et al. 2015a for details). The presence of baited traps during the radiotracking period may have caused an underestimation of home range size, similarly for both species and contexts.

Based on UD estimates, the home range overlaps between individuals of the same species were determined as the volume of intersection (VI; Seidel 1992) of UD for all pairs in a given study site (overlap computations were performed with a home-made Pascal program following the method described in Dufour et al. 2015a). The VI corresponds to the overlap area under the lower UD of the two individuals. Because UD were truncated at the 0.95 cumulative isopleth (to exclude poorly estimated UD tails), overlap values

were normalized between 0 and 1 by dividing VI by 0.95 (Benhamou et al. 2014 for details). The VI for each pair of individuals was calculated and averaged between members of a group (within-group VI values) and then compared to averaged overlaps between members of different groups (between-group VI values).

Statistics

All statistical analyses were conducted using R ver. 3 software (<www.r-project.org>). Significance levels were set at $\alpha=0.05$, and adjusted for multiple testing with the sequential (top-down) Bonferroni correction when necessary. Normality and heteroscedasticity of distributions were checked by plotting the model residuals; data were transformed when necessary.

To test the similarity of nest-site characteristics between the species and contexts (i.e. parapatry and sympatry), we performed χ^2 contingency table analyses with likelihood ratios. We assessed whether nest-sites used by a given mouse were randomly distributed by comparing within study site versus within individual nest-site distances using Wilcoxon tests (11 tests). A Spearman test was performed to assess the correlation between study site surface area and distance between occupied nest-sites.

Linear mixed-effect models were used to primarily test the influence of species and context on 1) log-transformed values of distance between used nest-sites, 2) nest-site fidelity, 3) group association strength, and 4) home range overlap. To account for pseudo-replication, all linear mixed-effect models included the study site identity (i.e. population) as a random factor (random intercepts), while sex differences were accounted for by adding sex as a fixed factor for individual-centered tested variables. To control for the potential influence of sex effect on analyses involving group characteristics (association strength and home range overlap), we calculated the sex-ratio of each group as the number of radio-tracked adult males divided by the total number of radio-tracked adults. We did not detect any significant variation of the sex-ratio between species, context and their interaction

(Table 5, Supplementary material Appendix 1 Table A3), and hence sex-ratio was not included in the analyses involving group characteristics.

The full models considered all the variables and interactions according to the species and the context (for all traits), the sex (for nest-site distance and fidelity), the group size (for AS), and the group state (intragroup versus intergroup for VI, Supplementary material Appendix 1 Table A3). The best-fitted model for each tested trait (and with random effect) was selected based on the Akaike weight (relative likelihood of a model to be the best among the set of models tested) and $\Delta AICc$ (Supplementary material Appendix 1 Table A3 for details about the models). Tukey HSD tests were used for pairwise post-hoc comparisons for significant fixed factors.

Data accessibility

Data deposited at the open archive HAL, hal-01912223 (Dufour et al. 2018).

Results

Nest-site characteristics

In parapatry, nest-site characteristics differed significantly between the two species (all comparisons $p < 0.001$, Table 4, Fig. 3). Nest-sites of *Rhabdomys bechuanae* were predominantly located inside bushes that were either alive or composed of a mixture of alive and dead vegetation, while the nest-sites of *R. d. dilectus* were exclusively in grass type vegetation (mostly alive). Moreover, nest-sites occupied by *R. d. dilectus* appeared to be more protected from predation than those occupied by *R. bechuanae*, the latter showing low to intermediate protection from predation (Fig. 2, 3).

In sympatry, the nest-sites of the two species also differed significantly in their external features, confirming selection for more woody type vegetation by *R. bechuanae* and more grass type vegetation by *R. d. dilectus* (Table 4, Fig. 3). However, nest-sites of *R. d. dilectus* also occurred in bare soil and woody

microhabitat and tended to show lower protection from predation compared to the nest-sites of *R. bechuanae* (Table 4, Fig. 3).

Nest-site characteristics of *R. bechuanae* did not vary significantly between parapatric and sympatric populations (Table 4), whereas those of *R. d. dilectus* were more diverse in their external features, offered significantly less predation protection and were composed of more mixed dead and alive vegetation in sympatry than in parapatry (Table 4, Fig. 3).

These results suggest selection of nest-sites with distinct characteristics by the two species when in parapatry, while some convergence occurred in sympatry due to *R. d. dilectus* occupying nest-sites more similar to those of *R. bechuanae* than to their parapatric counterparts.

Nest-site distribution

The distances between nest-sites used by a focal individual were not related to the study site surface area (Spearman correlation test $Rho = 0.22$, $p = 0.50$). Both in parapatry and in sympatry, the average distance between nest-sites used by a mouse was significantly lower than expected by random use of all nest-sites identified in a given site (Fig. 4, Supplementary material Appendix 1 Table A2, all $p < 0.001$). The distance between nest-sites occupied by a mouse was significantly greater for the males than for the females and for *R. bechuanae* females (10/35 being lactating) compared to *R. d. dilectus* ones (5/31 being lactating) in both contexts (Table 5A–B, Fig. 4). While the spatial distribution of nest-sites occupied was constrained for both species, *R. bechuanae* used more distantly-spaced nest-sites than *R. d. dilectus*.

Nest-site fidelity

Nest-site fidelity varied interactively between species and context (Table 5A). In parapatry, *R. bechuanae* showed significantly greater nest-site fidelity than *R. d. dilectus* (Table 5B, Fig. 5), while, in sympatry, nest-site fidelity did not differ between the two species (Table 5B). Sympatric populations

Table 4. Statistical results of contingency analyses of nest-site characteristics (external features, vegetation state and predation protection) comparing species and context (p-values which remained significant after application of the Bonferroni α sequential adjustment for multiple tests are indicated in bold).

Type of comparison	Statistic	External features	Vegetation state	Predation protection
Parapatry n = 218 (<i>R. bechuanae</i> versus <i>R. d. dilectus</i>)	χ^2	181.25	79.24	39.08
	df	3	2	2
	p	<0.001	<0.001	<0.001
Sympatry n = 58 (<i>R. bechuanae</i> versus <i>R. d. dilectus</i>)	χ^2	14.56	8.14	7.35
	df	3	2	2
	p	0.002	0.016	0.025
<i>R. bechuanae</i> n = 142 (parapatry versus sympatry)	χ^2	6.34	6.89	4.33
	df	3	2	2
	p	0.096	0.032	0.115
<i>R. d. dilectus</i> n = 134 (parapatry versus sympatry)	χ^2	49.12	100.81	74.11
	df	3	2	2
	p	<0.001	<0.001	<0.001

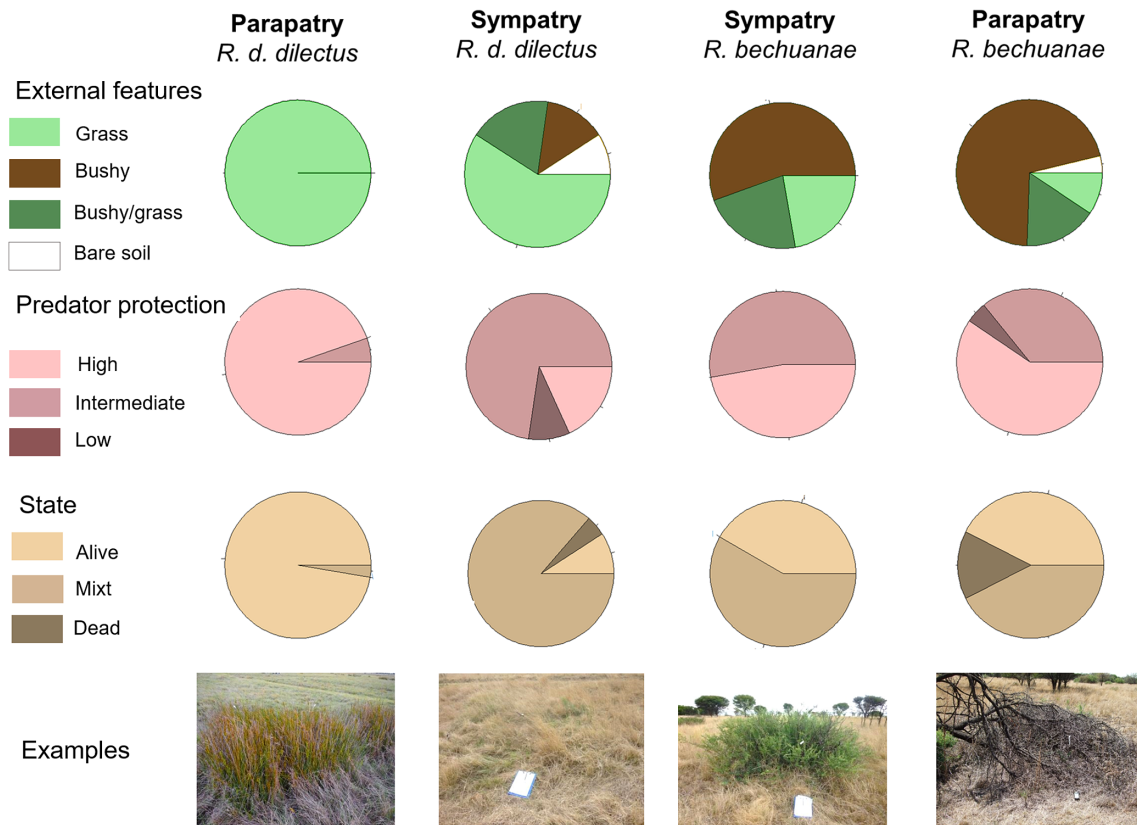


Figure 3. Comparisons of nest-site characteristics, determined from photographic analyses (an A4 white sheet is included for scale), by species and context.

of *R. d. dilectus* showed significantly higher fidelity than their parapatric counterparts (Table 5B), while *R. bechuanae* displayed similar nest-site fidelity in sympatry and parapatry (Table 5B, Fig. 5). However, although *R. bechuanae*

individuals exhibited high nest-site fidelity, most did not use exclusive nest-site, since they were observed to use at least two different nest-sites over a period of five or more days (fidelity index >0.2).

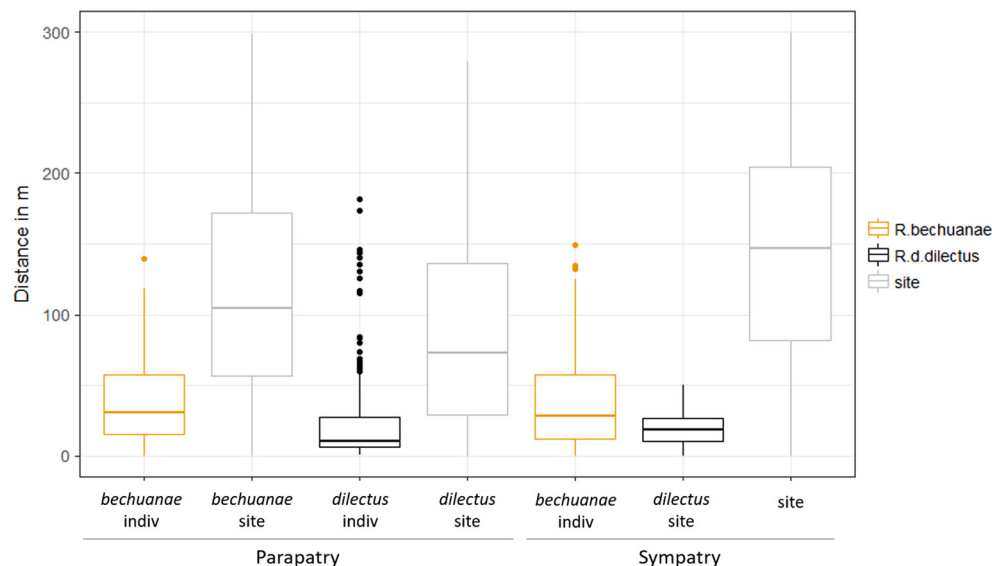


Figure 4. Pairwise distance in meters between all nest-sites used by a given individual (*R. d. dilectus* (in black) and *R. bechuanae* (in orange) or identified in each site (in grey) in both contexts (parapatry and sympatry). Box-plots show the median (thick line), first and third quartiles. The vertical lines indicate the lowest datum within 1.5 IQR (interquartile range) of the lower quartile, and the highest datum still within 1.5 IQR of the upper quartile. Individual dots represent outliers.

Table 5. Statistical results from the best-fitted linear mixed-effect models with random effects (A) for the distance (log transformed) between nest sites used by the individuals, nest-site fidelity, group association strength (AS), home range overlap (VI) and variation in radiotracked group sex-ratio. The full models considered all the variables and their interactions (Supplementary material Appendix 1 Table A3): species and context (for all models), sex (for nest-site distance and fidelity), group size (for AS), and group state (i.e. intragroup versus intergroup for VI). The site identity was set as a random effect (intercepts) in all models. The best-fitted models were then selected based on the Akaike information criterion (ΔAIC_c and weight, Supplementary material Appendix 1 Table A3). When an interaction was significant, Tukey post hoc tests were performed (B). Bold p-values highlight significant effects of the fixed variable.

Trait	Variable	Fixed/random	ndf	ddf	Value	SE	F	p-value
(A)								
Distance (log) between nest-sites used by individuals	(Intercept)		1	409	2.27	0.18	637.56	<0.001
	species	F	1	81	0.79	0.22	6.74	0.011
	context	F	1	12	-0.11	0.28	0.14	0.713
	sexe	F	1	81	0.66	0.17	8.43	0.005
	species:sexe	F	1	81	-0.62	0.25	5.95	0.017
Nest-site fidelity*	site indiv	R				0.42 ^a	71.46 ^b	<0.001
	(Intercept)		1	101	0.70	0.03	780.24	<0.001
	species	F	1	101	-0.25	0.04	28.82	<0.001
	context	F	1	12	-0.22	0.07	4.92	0.047
	species:context	F	1	101	0.20	0.08	6.14	0.015
AS	site	R				0.03 ^a	0.24 ^b	0.623
	(Intercept)		1	130	0.27	0.04	216.42	<0.001
	species	F	1	130	0.15	0.05	4.03	0.047
	context	F	1	12	0.19	0.09	0.82	0.384
	species:context	F	1	130	-0.25	0.12	4.13	0.044
VI*	site	R				0.07 ^a	2.21 ^b	0.137
	(Intercept)		1	129	8.55	2.50	337.56	<0.001
	species	F	1	129	-2.32	3.26	1.86	0.175
	context	F	1	12	9.64	6.73	0.37	0.553
	group state	F	1	129	41.15	2.72	231.67	<0.001
SR	species:context	F	1	129	-13.94	8.88	2.47	0.119
	site	R				2.00 ^a	0.17 ^b	0.677
	(Intercept)		1	131	0.37	0.05	159.59	<0.001
	species	F	1	131	0.09	0.07	1.72	0.192
	context	F	1	12	-0.02	0.09	0.03	0.862
	site	R				0.09 ^a	7.93 ^b	0.005
Trait	Tukey test (lower; upper confident interval 95%)			Estimate	SE	df	t ratio	p-value
(B)								
Distance nest-sites (log)	<i>R. d. dilectus</i>. Female (1.79; 2.63)	<i>R. bechuanae</i>. Female (2.62; 3.39)		-0.79	0.22	81	-3.64	<0.001
	<i>R. d. dilectus</i> . Male (2.44; 3.30)	<i>R. bechuanae</i> . Male (2.61; 3.47)		-0.17	0.23	81	-0.72	0.473
Nest-site fidelity	<i>R. d. dilectus</i>. Parapatry (0.63; 0.77)	<i>R. bechuanae</i>. Parapatry (0.38; 0.51)		0.25	0.04	101	5.77	<0.001
	<i>R. d. dilectus</i>. Parapatry (0.63; 0.77)	<i>R. d. dilectus</i>. Sympatry (0.35; 0.60)		0.22	0.07	12	3.33	0.030
AS	<i>R. bechuanae</i> . Parapatry (0.38; 0.51)	<i>R. bechuanae</i> . Sympatry (0.32; 0.53)		0.02	0.06	12	0.31	0.990
	<i>R. d. dilectus</i> . Sympatry (0.35; 0.60)	<i>R. bechuanae</i> . Sympatry (0.32; 0.53)		0.05	0.07	101	0.71	0.890
	<i>R. d. dilectus</i>. Parapatry (0.19; 0.36)	<i>R. bechuanae</i>. Parapatry (0.34; 0.50)		-0.15	0.05	130	-2.72	0.008
	<i>R. d. dilectus</i> . Sympatry (0.29; 0.64)	<i>R. bechuanae</i> . Sympatry (0.19; 0.53)		0.10	0.11	130	0.92	0.360

^aStandard deviation.

^bLikelihood ratio.

*The best-fitted models did not include the random effect (Supplementary material Appendix 1 Table A3) but to consider pseudo-replication, we provided the best models with the random factor. The models with and without the random effect generated the same general results (Supplementary material Appendix 1 Table A4).

Group association strength based on frequency of nest-site sharing

Rhabdomys bechuanae displayed greater group association strength (AS) than *R. d. dilectus* in parapatry (Table 5B), but not in sympatry (Table 5B) where *R. d. dilectus* group association strength was as high as that of *R. bechuanae* (Fig. 6).

In both species, groups of more than three individuals were observed in the two contexts, and groups of more than four individuals in parapatry (group size was similar between the species and contexts): among the 83 groups (i.e. comprising a

minimum of two radiotracked mice; 44 *R. d. dilectus* and 39 *R. bechuanae*), 22 (13 *R. d. dilectus* and 9 *R. bechuanae*) were composed of three to five adults.

Home range overlaps: a validation of group membership

Home range overlaps (VI) were significantly greater between members of the same group than between members of different groups (Table 5A, Fig. 7). This result did not differ significantly between species and was consistent across contexts (i.e. parapatry versus sympatry; Table 5A).

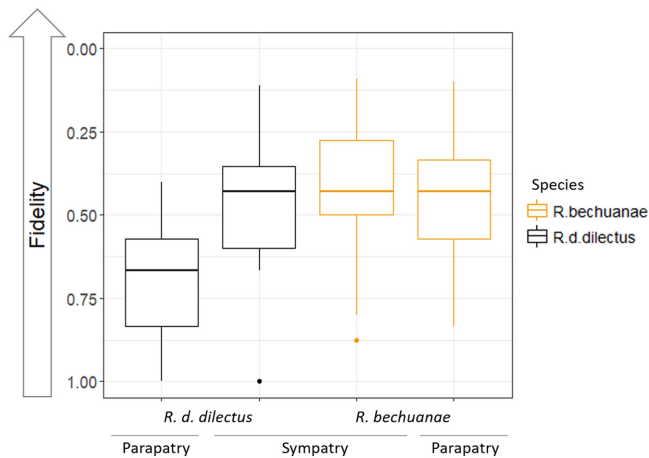


Figure 5. Nest-site fidelity assessed as the ratio of number of nest-site used/number of nights when *R. d. dilectus* (in black) and *R. bechuanae* (in orange) individuals were radiotracked in parapatry and sympatry. A score of 1 indicates use of a different nest-site each night. Box-plots show the median (thick line), first and third quartiles. The vertical lines indicate the lowest datum within 1.5 IQR (interquartile range) of the lower quartile, and the highest datum still within 1.5 IQR of the upper quartile. Individual dots represent outliers.

Moreover, home range overlap between group members was positively correlated with their group association strength index (Spearman Rho=0.311, $p=0.009$), further validating our assessment of group membership and cohesion based on nest-site occupancy. These results suggest that group members share a territory and avoid those of other groups, a pattern confirmed in sympatry.

Discussion

Consistent with their microhabitat selection (Dufour et al. 2015a), the two *Rhabdomys* species selected distinct nest-site types in parapatry and more similar ones in sympatry. Further, as revealed by our approach using two indirect but complementary proxies of sociality – nest-site sharing and home-range overlaps – both species displayed group living in parapatry and sympatry, although *R. bechuanae* showed greater group cohesion than *R. d. dilectus* in parapatry. High nest-site fidelity and group association strength, as displayed by *R. bechuanae* in parapatry and both species in sympatry, suggest the importance of microhabitat features and predation (i.e. open habitat and relatively exposed nest-sites) as facilitators of group living and cohesion. However, compared to *R. bechuanae*, slightly less protective and more clumped nest-sites occupied by *R. d. dilectus* in sympatry suggest that species interference may constrain *R. d. dilectus* movement and indirectly force group living and cohesion. Altogether, our study shows the importance of microhabitat features in shaping *Rhabdomys* social organization and points out for the first time that species interference, by constraining space use, may contribute to evolution of social organization (Table 1).

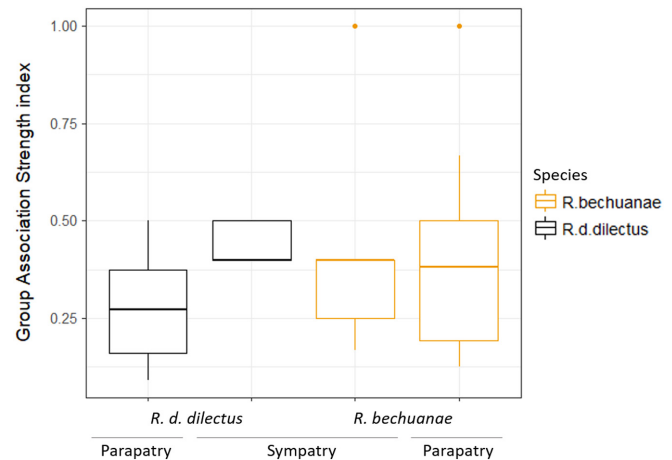


Figure 6. Group association strength index according to species (*R. d. dilectus* in black; *R. bechuanae* in orange) and context (parapatry and sympatry). Box-plots show the median (thick line), first and third quartiles. The vertical lines indicate the lowest datum within 1.5 IQR (interquartile range) of the lower quartile, and the highest datum still within 1.5 IQR of the upper quartile. Individual dots represent outliers.

Microenvironment impacts social organization

The patchiness of resources in general, and of nest-sites and shelters in particular, is often considered as a driver of sociality. For instance, greater nest-site fidelity, greater home range overlaps between relatives and larger social groups are among the observed responses to habitat fragmentation in the bank vole (*Clethrionomys glareolus*; Mappes et al. 1995), coyote

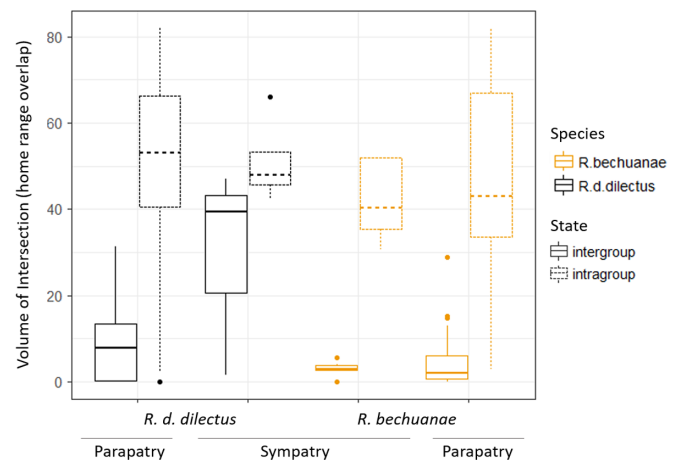


Figure 7. Volume of intersection (VI, area in m²) of home range overlaps between members of the same nest-site group (intragroup, dashed lines) versus between members of different groups (intergroup, solid lines) according to species (*R. d. dilectus* in black; *R. bechuanae* in orange) and context (parapatry and sympatry). Box-plots show the median (thick line), first and third quartiles. The vertical lines indicate the lowest datum within 1.5 IQR (interquartile range) of the lower quartile, and the highest datum still within 1.5 IQR of the upper quartile. Individual dots represent outliers.

Canis latrans (Atwood and Weeks 2003) and Cunningham's skink *Egernia cunninghami* (Stow and Sunnucks 2004). Consistent with these general findings, in parapatry, the nest-site fidelity and group association strength were higher in *R. bechuanae* occupying habitats characterized by patchily distributed vegetation and nest-sites, compared to *R. d. dilectus* found mostly in continuous habitats with important cover (Dufour et al. 2015a).

Both *R. d. dilectus* and *R. bechuanae* selected nest-sites significantly closer together than expected by chance. Space use is shaped by mobility, territoriality, environmental features, foraging and predation risk (Börger et al. 2008). In terms of mobility, the sampled surface area of each site in our study was small enough to be explored by both *R. bechuanae* and *R. d. dilectus* under ideal free conditions. However, the patterns of home range overlap observed in both species (i.e. larger overlaps within group members than between groups and positive correlation between association strength and home-range overlap) suggest that territoriality between groups may limit space use and hence may impact the distance between nest-sites occupied by an individual or a group. Further, the distances between nest-sites used by a focal individual (both species), being smaller than expected by chance, might reflect sufficient and clumped distribution of resources in our study sites, refuting the limited foraging resource hypothesis as an explanation of the observed species space use (Silk et al. 2014).

Rhabdomys d. dilectus females used a more clustered network of nest-sites than *R. bechuanae* females in both contexts. Clustered nesting may represent a way to reduce exposure to predators (e.g. reduce mobility in open area). However, the perception of predation risk may also favor the use of more distant nest-sites that could serve as refuges, particularly when the nest-sites are more exposed to predation (Godsall et al. 2013), which is the case for *R. bechuanae* and both species in sympatry. Radespiel et al. (2003) reported that while the social mouse lemur species – *Microcebus murinus* – slept in protected and sheltered nest-sites, *M. ravelobensis* formed smaller sleeping social groups in open vegetation and less protected sleeping sites with frequent nest switching. These authors attributed differences in social behavior and nest-site utilization to the ecological divergence between the species in allopatry, as a result of different thermoregulation and predation strategies. Our study reveals that evolution under distinct ecological conditions may have also resulted in different nesting characteristics in the two striped mouse species, although, unlike for the mouse lemur, greater nest fidelity and higher group association strength were associated with less protected and more distant nest-sites. These contrasting responses indicate that although the environment influences sociality (Lacey and Sherman 2007, Webber and Vander Wal 2018), its precise consequences may not be generalizable across species.

The natural setting of our experiments allowed for direct comparisons of the two species under similar environmental conditions (grassland and shrubland microhabitats being

available in all sites; Dufour et al. 2015a). Therefore, the finding that they selected distinct microhabitats and nest-site types in parapatry strongly suggests divergence during evolution in allopatry and possibly divergent adaptation (e.g. boldness or mobility in open risky habitat type). Further, the fact that *R. d. dilectus* could thrive in habitats similar to *R. bechuanae* in sympatry and adjust its social organization suggests its flexibility.

Species interference and evolution of sociality

In sympatry, the shift in microhabitat selection observed in *R. d. dilectus* was associated with greater nest-site fidelity and higher group association strength. Dooley and Dueser (1996) attributed the change of sleeping sites in *Peromyscus leucopus* in terms of the external features (from tree to ground) and quality (nesting on ground is less favorable to winter survival and predator protection) to competition for nest-sites with the dominant *P. maniculatus*.

Greater nest-site fidelity and group cohesion of *R. d. dilectus* observed in sympatry could be the result of either interspecific competition (or its indirect impact on intraspecific competition), predation (indirect influence of microhabitat selection), or both: fewer nest-sites available for *R. d. dilectus* and high perceived predation risks in a relatively open habitat may limit its movements. Indeed, *R. d. dilectus* individuals occurring in grassland avoided open woody patches even when they were supplemented with food (Abu Baker and Brown 2010). In addition, in another study involving the same populations of *R. bechuanae* and *R. d. dilectus*, home-range overlap between the species in sympatry was significantly lower than expected by chance, further suggesting that interspecific competition could occur (Dufour et al. 2015a). Moreover, in sympatry, *R. bechuanae* are significantly heavier than similar sized *R. d. dilectus* adults (Ganem et al. unpubl.) which suggest they may dominate *R. d. dilectus*. Finally, although potential breeders of the two species can discriminate between conspecifics and heterospecifics, they still do engage in mating attempts with the other species (Dufour et al. 2015b). Thus, it appears plausible that during the breeding season and in sympatry, interspecific competition for both mates and nest-sites may occur and limit the access of *R. d. dilectus* to shelters (numbers and quality). Such competition could explain the slightly lower quality nest-site occupied and relatively low mobility of *R. d. dilectus*, particularly of females, compared to *R. bechuanae* under the same conditions. Additional studies during the non-breeding season, when competition is expected to be low, would allow us to disentangle the relative role of habitat versus competition in shaping social organization of *R. d. dilectus* in sympatry.

Social variation within the genus *Rhabdomys*

The genus *Rhabdomys* radiated along a climatic gradient in southern Africa, ranging from the dry and open environment

of the west–northwest to mesic and grassland vegetation in the east (Meynard et al. 2012, du Toit et al. 2012). It has long been considered as a monospecific genus, showing population-level variations in social behavior ascribed to variable environmental conditions: open, patchy and dry environment favoring group-living as opposed to mesic continuous grassland hosting solitary individuals (Schradin and Pillay 2005, Schoepf and Schradin 2012).

A literature survey (Supplementary material Appendix 1 Table A1) indicates that the two semi-arid striped mouse species, *R. bechuanae* and *R. pumilio*, are more social than their two mesic counterparts, *R. d. dilectus* and *R. d. chakae*, confirming the general view of the impact of environmental conditions on evolution of social behavior (Lacey and Sherman 2007, Silk 2007, Schradin 2013, Gardner et al. 2015). *Rhabdomys bechuanae* has been described as socially tolerant at the core of its distribution (Kalahari; Supplementary material Appendix 1 Table A1), and the present study shows that this also applies at the distribution margins of the species. However, unlike *R. pumilio* whose social groups occupy a single nest-site (Schradin and Pillay 2004, Schradin 2013), *R. bechuanae* seems to display a fission–fusion group structure type (Couzin 2006), suggesting lower group cohesion and sociality compared to *R. pumilio* (Schradin 2013). Differences in sociality between the two species may be an indication that they experience different environmental constraints, a hypothesis that could be tested in the future. In particular, the aridity food distribution hypothesis (AFDH) offers a possible theoretical model to consider evolution of sociality in the genus *Rhabdomys*. In mole rat species, the AFDH suggests that more complex social organization evolved under arid environments and patchy distribution of food (Jarvis et al. 1994).

Conclusions

Habitat characteristics and their impact on nest-site quality and distribution appear to be important drivers of social divergence in the genus *Rhabdomys*. Moreover, at least two *Rhabdomys* species – *R. d. dilectus* (this study) and *R. pumilio* (Schoepf and Schradin 2012) – adjust some aspects of their social behavior in response to environmental constraints. Importantly, the present study introduced the idea that interspecific competition may generate novel environmental pressures, by restricting individual movements and constraining nest-site sharing, which could influence the social organization of species. Consequently, the role of interspecific competition on social evolution appears as a promising avenue of future research.

Acknowledgments – This study benefitted from discussions with Yasmin Latour and Inbar Maayan as well as field work assistance from Camille Rioux, Julie Perez, Jurie du Plessis and the personnel of the different reserves. We particularly thank Simon Benhamou for his input in home range analyses, and Simon Chamaille-Jammes for the loan of camera traps.

Funding – We acknowledge the financial support of the doctoral school of Montpellier SIBAGHE, as well as French/SA agreements through PICs (no. 4841, no. 81859) GDRI (no. 191) and the LIA RhabAdapt. ISEM 2018-227.

Permits – This study followed the ABS/ASAB guidelines for ethical treatment of animals, and care was taken to ensure the well-being of the mice throughout the duration of the study. Permits to trap, handle and fit striped mice with radio collars were obtained from the French ethics authorities (C34–265) and Animal Ethics Screening Committee of Witwatersrand University (ethics number AESC 2012/13/2A), and from the ethics authorities of the Free State (no. 01/15700) and North–West provinces (no. 01/11262), South Africa.

References

- Abu Baker, M. A. and Brown, J. S. 2010. Islands of fear: effects of wooded patches on habitat suitability of the striped mouse in a South African grassland. – *Funct. Ecol.* 24: 1313–1322.
- Atwood, T. C. and Weeks, H. P. 2003. Spatial home-range overlap and temporal interaction in eastern coyotes: the influence of pair types and fragmentation. – *Can. J. Zool.* 1597: 1589–1597.
- Auclair, Y. et al. 2014. Nest attendance of lactating females in a wild house mouse population: benefits associated with communal nesting. – *Anim. Behav.* 92: 143–149.
- Banda, E. and Blanco, G. 2009. Implications of nest-site limitation on density-dependent nest predation at variable spatial scales in a cavity-nesting bird. – *Oikos* 118: 991–1000.
- Benhamou, S. et al. 2014. Movement-based analysis of interactions in African lions. – *Anim. Behav.* 90: 171–180.
- Börger, L. et al. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. – *Ecol. Lett.* 11: 637–650.
- Couzin, I. 2006. Behavioral ecology: social organization in fission–fusion societies. – *Curr. Biol.* 16: 169–171.
- Dooley, J. L. and Dueser, R. D. 1996. Experimental tests of nest site competition in two *Peromyscus* species. – *Oecologia* 105: 81–86.
- du Toit, N. et al. 2012. Biome specificity of distinct genetic lineages within the four-striped mouse *Rhabdomys pumilio* (Rodentia: Muridae) from southern Africa with implications for taxonomy. – *Mol. Phylogenet. Evol.* 65: 75–86.
- Duckworth, R. A. et al. 2015. Cycles of species replacement emerge from locally induced maternal effects on offspring behavior in a passerine bird. – *Science* 347: 875–877.
- Dufour, C. M. S. et al. 2015a. Space use variation in co-occurring sister species: response to environmental variation or competition? – *PLoS One* 10: 1–15.
- Dufour, C. M.-S. et al. 2015b. Ventrō–ventral copulation in a rodent: a female initiative? – *J. Mammal.* 95: 1017–1023.
- Dufour, C. M. S. et al. 2017. Ecological character displacement between a native and an introduced species: the invasion of *Anolis cristatellus* in Dominica. – *Biol. J. Linn. Soc.* 123: 43–54.
- Dufour, C. M. S. et al. 2018. Data from: habitat characteristics and species interference influence space use and nest-site occupancy: implications for social variation in two sister species. – HAL Open Repository, hal-01912223.
- Ebensperger, L. A. et al. 2008. Activity, range areas and nesting patterns in the viscacha rat, *Octomys mimax*. – *J. Arid Environ.* 72: 1174–1183.

- Edelman, A. J. et al. 2009. Potential for nest site competition between native and exotic tree squirrels. – *J. Mammal.* 90: 167–174.
- Forstmeier, W. and Weiss, I. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. – *Oikos* 104: 487–499.
- Ganem, G. et al. 2012. Environmental correlates and co-occurrence of three mitochondrial lineages of striped mice (*Rhabdomys*) in the Free State province (South Africa). – *Acta Oecol.* 42: 30–40.
- Gardner, M. G. et al. 2015. Group living in squamate reptiles: a review of evidence for stable aggregations. – *Biol. Rev.* 91: 925–936.
- Godsall, B. et al. 2013. From physiology to space use: energy reserves and androgenization explain home-range size variation in a woodland rodent. – *J. Anim. Ecol.* 83: 126–135.
- Grant, P. R. 1972. Convergent and divergent character displacement. – *Biol. J. Linn. Soc.* 4: 39–68.
- Grether, G. F. et al. 2009. The role of interspecific interference competition in character displacement and the evolution of competitor recognition. – *Biol. Rev. Camb. Phil. Soc.* 84: 617–35.
- Hayes, L. 2000. To nest communally or not to nest communally: a review of rodent communal nesting and nursing. – *Anim. Behav.* 59: 677–688.
- Heap, S. and Byrne, P. G. 2013. Aggregation and dispersal based on social cues as a nest-site selection strategy in a resource-defence polygynandry mating system. – *Behav. Ecol. Sociobiol.* 67: 685–697.
- Holway, D. A. and Suarez, A. V. 1999. Animal behavior: an essential component of invasion biology. – *Trends Ecol. Evol.* 14: 328–330.
- Jarvis, J. et al. 1994. Mammalian eusociality: a family affair. – *Science* 9: 1–5.
- Kappeler, P. M. and Schaik van, C. P. 2002. Evolution of primate social systems. – *Int. J. Primatol.* 23: 707–740.
- Kotler, B. et al. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. – *Ecology* 72: 2249–2260.
- Lacey, E. A. and Sherman, P. 2007. The ecology of sociality in rodents. – In: Wolff, J. O. and Sherman, P. W. (eds), *Rodent societies: an ecological and evolutionary perspective*. Univ. of Chicago Press, pp. 243–254.
- Latour, Y. and Ganem, G. 2017. Does competitive interaction drive species recognition in a house mouse secondary contact zone? – *Behav. Ecol.* 28: 212–221.
- Lichtenstein, J. L. L. et al. 2017. The multidimensional behavioural hypervolumes of two interacting species predict their space use and survival. – *Anim. Behav.* 132: 129–136.
- Mainwaring, M. C. et al. 2017. Climate change and nesting behaviour in vertebrates: a review of the ecological threats and potential for adaptive responses. – *Biol. Rev.* 92: 1991–2002.
- Mappes, T. et al. 1995. Higher reproductive success among kin groups of bank voles (*Clethrionomys glareolus*). – *Ecology* 76: 1276–1282.
- Meynard, C. N. et al. 2012. Evidence of environmental niche differentiation in the striped mouse (*Rhabdomys* sp.): inference from its current distribution in southern Africa. – *Ecol. Evol.* 2: 1008–1023.
- Pfennig, K. S. and Pfennig, D. W. 2009. Character displacement: ecological and reproductive responses to a common evolutionary problem. – *Q. Rev. Biol.* 84: 253–276.
- Pillay, N. 2000. Fostering in the African striped mouse: implications for kin recognition and dominance their own offspring, and in doing so must distinguish between their own and to their own offspring (i.e. do not participate in communal nursing). For example, al. 1. – *Acta Theriol.* 45: 193–200.
- Radespiel, U. et al. 2003. Species-specific usage of sleeping sites in two sympatric mouse lemur species (*Microcebus murinus* and *M. ravelobensis*) in northwestern Madagascar. – *Am. J. Primatol.* 59: 139–151.
- Rangel, J. et al. 2010. Nest-site defense by competing honey bee swarms during house-hunting. – *Ethology* 116: 608–318.
- Santos, J. W. A. and Lacey, E. A. 2011. Burrow sharing in the desert-adapted torch-tail spiny rat, *Trinomys yonenagae*. – *J. Mammal.* 92: 3–11.
- Schoepf, I. and Schradin, C. 2012. Better off alone! Reproductive competition and ecological constraints determine sociality in the African striped mouse (*Rhabdomys pumilio*). – *J. Anim. Ecol.* 81: 649–656.
- Schooley, R. L. et al. 1996. Can shrub cover increase predation risk for a desert rodent? – *Can. J. Zool.* 7: 157–163.
- Schradin, C. 2005. Nest-site competition in two diurnal rodents from the succulent karoo of South Africa. – *J. Mammal.* 86: 757–762.
- Schradin, C. 2006. Whole-day follows of striped mice (*Rhabdomys pumilio*), a diurnal murid rodent. – *J. Ethol.* 24: 37–43.
- Schradin, C. 2013. Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. – *Phil. Trans. R. Soc. B* 368: 20120346.
- Schradin, C. and Pillay, N. 2004. The striped mouse (*Rhabdomys pumilio*) from the succulent karoo, South Africa: a territorial group-living solitary forager with communal breeding and helpers at the nest. – *J. Comp. Psychol.* 118: 37–47.
- Schradin, C. and Pillay, N. 2005. Intraspecific variation in the spatial and social organization of the african striped mouse. – *J. Mammal.* 86: 99–107.
- Schradin, C. et al. 2006. Winter huddling groups in the striped mouse. – *Can. J. Zool.* 84: 693–698.
- Seidel, K. 1992. Statistical properties and applications of a new measure of joint space use for wildlife. – PhD thesis, Univ. of Washington, Seattle, WA.
- Silk, J. B. 2007. The adaptive value of sociality in mammalian groups. – *Phil. Trans. R. Soc. B* 362: 539–559.
- Silk, M. J. et al. 2014. The importance of fission–fusion social group dynamics in birds. – *Ibis* 156: 701–715.
- Stow, A. J. and Sunnucks, P. 2004. High mate and site fidelity in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. – *Mol. Ecol.* 13: 419–430.
- VanderWaal, K. L. et al. 2013. Multilevel social organization and space use in reticulated giraffe (*Giraffa camelopardalis*). – *Behav. Ecol.* 25: 17–26.
- Violle, C. et al. 2011. Phylogenetic limiting similarity and competitive exclusion. – *Ecol. Lett.* 14: 782–787.
- Webber, G. M. R. and Vander Wal, E. 2018. An evolutionary framework outlining the integration of individual social and spatial ecology. – *J. Anim. Ecol.* 87: 113–127.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. – *Ecology* 70: 164–168.

Supplementary material (available online as Appendix oik-05357 at <www.oikosjournal.org/appendix/oik-05357>). Appendix 1.